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Breeding male grey seals exhibit similar activity budgets across varying exposures to human activity

Running Head: Male gray seal activity budgets

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Human-wildlife interactions can be incidental or direct through activities such as wildlife-tourism. In the presence of anthropogenic activities, some animals exhibit behavioural alterations such as increased vigilance or spatial displacement. Thus, chronic exposure could be adverse to individual fitness through loss of energy or time. Pinnipeds are exposed to human activities in the aquatic environment and on land, but the degree of exposure varies across a species' geographic distribution. For example, breeding colonies of grey seals (*Halichoerus grypus*) along the mainland coast of England are exposed to anthropogenic disturbance in the forms of tourism and military activities; however, many offshore colonies are relatively undisturbed. Due to the recent expansion of mainland colonies, the impacts of human presence during the breeding season are of urgent interest for managers. Therefore, the aim of this study was to test for any behavioural adjustments associated with anthropogenic presence by comparing the activity budgets of individual male grey seals at a mainland colony, with activity budgets from two isolated colonies. We found no evidence of differences in the male activity budgets for time spent in Non-Active behaviours across colonies, and of the three colonies, males on the mainland spent the least amount of time Alert. This indicates that as capital breeders, selection for conservation of energy is potentially overriding short-term costs of local stressors or that males at the mainland colony have habituated to the human presence. We further provide discussion of the management implications of our findings. *[Keywords: wildlife tourism, Halichoerus grypus, behaviour, conservation, management]*

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INTRODUCTION

Human population growth has been associated with increased human-wildlife interactions (Treves & Karnth 2003, Converse et al. 2005), particularly in coastal regions. According to the United States 2011 census, in 2010 coastal counties accounted for < 10 % of land area (excluding Alaska), but 39% of the population; a 39% increase since 1970 (US census data; NOAA). This overlap of human and wildlife spatial usage in coastal regions drives unintentional interactions such as manatee strikes (Jett et al. 2013) or fisheries bycatch (Lewison et al. 2014), but also can promote intentional interactions such as wildlife-tourism (Hardiman & Burgin 2010, Velando & Munilla 2011, Curtin 2013, Le Boeuf & Campagna 2013, Mustika et al. 2013). Marine wildlife tourism is a multi-million dollar industry world-wide. For example, in 2010 reports from Scotland indicated that marine wildlife tourism had a net economic impact of around £65M (equivalent to$110M US; SGSR 2010). In most cases, organized wildlife tourism operates under the ethos of sustainable, non-invasive and conservation-minded wildlife viewing and the public responds positively to these measures (Ballantyne et al. 2009, Le Boeuf & Campagna 2013). To ensure sustainability, many government organizations, non-profit organizations or associations of tour operators work with scientists to generate self-enforced viewing guidelines (Hoover-Miller et al. 2013). However, even when ecotourism is promoted under such 'best intentions', critics argue that there is a potential for cumulative adverse effects to animals' fitness from these activities (Duffus & Dearden 1990, Williams et al. 2006, Catlin et al. 2011, Christiansen et al. 2013).

One group of animals which has high exposure to human interactions is the phocid seals. Species within this group face exposure to human activities at sea while foraging (Skeate et al. 2012) and on land during breeding, moulting and resting periods (Perry et al. 2002, Curtin et al. 2009, Le Boeuf & Campagna 2013, Granquist & Sigurjonsdottir 2014). Many studies have focused on determining the effects of disturbance during critical periods such as pupping or moulting. Altered behavioural states during these times could be placing an energetic cost on seals resulting in long-term repercussions or a reduction in fitness (Suryan & Harvey 1999, Lewis & Matthews 2000, Perry et al. 2002, Engelhard et al. 2002, Stevens & Boness 2003, Curtin et al. 2009, Granquist & Sigurjonsdottir

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2014). At sea, disturbances can lead to lost foraging opportunities and/or increased energetic costs through physiological or behavioural alterations associated with avoidance behaviours (Williams et al. 2006, Christiansen et al. 2013). As capital breeders, the potential for increased energy expenditure due to disturbance while on land is also important to consider, as most phocids are energetically limited during their time ashore to reserves previously gained during the foraging season. For males in particular, the ability to prolong the length of stay on the colony during fasting is strongly correlated with mating and reproductive success (Twiss 1991, Lidgard et al. 2004, Twiss et al. 2006) and any disturbances during these discrete life history periods could lead to reduced individual fitness. How individuals respond to disturbances, whether on land or at sea, will likely be determined by the ecological landscape, level of exposure to tourism activities, and individual differences in tolerance to disturbances (Bejder et al. 2009, Bennett et al. 2013, Christiansen et al. 2013, Christiansen et al. 2015).

Grey seals (*Halichoerus grypus*) are a species of phocid which occupies a wide geographic range, breeds across a variety of substrates, and demonstrates variability in behaviours in response to topography and weather, across and within sites (Boness 1984, Anderson & Fedak 1985, Twiss 1991, Lawson 1993). Many of the studies investigating the ecology and behaviour of this species have been conducted on populations breeding on offshore islands in remote places such as northern Scotland (e.g. North Rona and the Monach Islands, Fig 1) or Eastern Canada (Sable Island, Fig 1). However, since the mid-1990s, there has been a remarkable expansion of grey seal breeding distributions along the eastern, mainland coast of England and a parallel expansion south along the eastern US coast (Duck &Morris 2010, NEFSC 2010). As such, haul-out sites and breeding colonies now persist in areas of greater human densities, such as around the Thames Estuary near London (Barker et al. 2014). One such breeding colony is Donna Nook; located on the mainland coast of England just south of the Humber Estuary (53.47°N, 0.15°E) (Fig 1). The site is managed as a part of the Lincolnshire Wildlife Trust's wildlife refuge system and the Defence Infrastructure Organisation (DIO) air force training range. Since the mid-1990s, the colony has experienced rapid population growth with pup production increasing at rates of 5-40% between 1990 and 2014 (Duck & Morris 2010). As a mainland colony, Donna Nook is exposed to various levels of anthropogenic activity. The northern

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87 section of the colony is open to public viewing access. Visitors gather during the breeding season to
88 view and photograph the seals but physical contact with and proximity to the seals is restricted by a
89 wooden double fence and by Wildlife Trust wardens. Due to the presence of the DIO base, the
90 southern extent of the colony is off limits to visitor access, and human presence is limited to
91 operational necessities. Throughout the breeding season, on weekdays, the colony as a whole is
92 exposed to anthropogenic noise from military training exercises, usually consisting of periodic jet or
93 helicopter flyovers.

94 Humans and human activities are often a part of the ecological system in which grey seal
95 foraging and breeding occurs. Studying the behaviours of animals can reveal how this aspect of the
96 environment influences behavioural choices and ultimately impacts fitness. Previous studies
97 investigating the effects of human activities on grey seal behaviours have focused on non-terrestrial
98 forms of disturbance; either noise-pollution (Perry et al. 2002) or vessel-based viewing platforms
99 (Curtin et al. 2009, Strong & Morris 2010) and the results are inconclusive. For example, Curtin et al.
100 (2009) found that, when wildlife viewing vessels were in close proximity, groups of grey seals (mixed
101 age and sex-classes) at a haul-out site exhibited greater rates of alert behaviours. In contrast, Perry et
102 al. (2002) found no evidence that adult male or female grey seals were responding behaviourally to
103 sonic booms during the breeding season. These differences could represent changes in behavioural
104 patterns across life history stages (breeding vs. non-breeding) (Pavez et al. 2014); however, both of
105 these examples focused on a single breeding or haul-out location and tested for acute response/no-
106 response effects of anthropogenic activities. Our aim was to extend the scope of such questions by
107 utilizing data from across the geographic range of the grey seal to encompass as much of the natural
108 variation in the behavioural ecology of this species as possible.

109 To do this, we compared activity budgets of males breeding on a mainland colony to males at
110 colonies with historically little to no human presence and examined if there appeared to be any cross-
111 sectional behavioural indication of disturbance from terrestrial-based, anthropogenic activities.
112 Studies from other animal systems have suggested that the presence of anthropogenic activities,
113 including wildlife tourism, can increase the amount of time animals spend in vigilance and anti-
114 predator behaviours within a population (Frid & Dill 2002, Holcomb et al. 2009, Côté et al. 2013).

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Bottlenose dolphins (*Tursiops truncatus)* in the presence of tourism boats had reduced amounts of time and number of bouts of resting and socializing (Lusseau 2003), harbour porpoises (*Phocoena phocoena*) exposed to geological seismic surveying noise showed reduced vocalizations (Pirotta et al. 2014), and caribou herds (*Rangifer tarandus caribou*) in the presence of tourists were found to spend more time vigilant and standing at the expense of time spent resting (Duchesne et al. 2000). Based on these patterns, if seals at Donna Nook are exhibiting chronic anti-predator disturbance behaviours, we might assume individuals to be more active or vigilant across a breeding season than individuals from the more remotely located colonies. To test our hypothesis, we compared activity budgets for males at Donna Nook to males at North Rona and Sable Island (Twiss 1991); both of which are offshore colonies where the only human presence during the breeding season is associated with research. Specifically, we predict that time males spend in Non-Active behaviours will be lowest and time spent alert will be greatest at Donna Nook in comparison to males at North Rona and Sable Island.

METHODS

Description of breeding colonies

Donna Nook is characterized by tidally influenced, estuarine topography. To the north, tidal marshes transition into a mixture of grassy dunes, muddy wallows and man-made paths consisting of primarily tamped sand. The remainder, and vast majority, of the colony is a sand-flat with little to no topographic variation or vegetation. The entire colony is bordered on the south/western extent by high dunes and thick vegetation. During the breeding season, two aggregations form: the outer aggregation along the shoreline and the inner, or main, breeding aggregation which is distributed farther landward with clustering near the dune-line. Seals often use tidal channels to move from the sea to locations across the sand flats. Sable Island (Canada) is topographically most similar to Donna Nook in some places. It is characterized by relatively unrestricted access and broad expanses of uniform flat sand around the periphery. Intricate dune assemblages occur centrally along some parts of the island (Boness & James 1979, Twiss 1991, Twiss et al. 1994). In contrast, North Rona has variable elevation up to 108m (Twiss 1991). On the western coast, the high cliffs offer no access points and seals must

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142 access the breeding colony from four main gullies located on the eastern side. Once on the main
143 breeding grounds, the vegetation is predominantly grassland interspersed with permanent and
144 ephemeral freshwater pools, erratic stones and remnants of dry stone walls (Anderson et al. 1975,
145 Twiss 1991, Twiss et al. 1994, Pomeroy et al. 1994).

146 ***Donna Nook general data collection***

147 Field observations were conducted during all daylight hours (mean = 8h 48min daily) across
148 two autumn breeding seasons from 3 November to 12 December in 2011, and from 27 October – 12
149 December in 2012. The breeding colony was split into two study sites to cover the range of
150 topography: the PUB site with grassy dunes and mud wallows (53.476°N, 0.155°E) and the RAF site
151 which was primarily comprised of sand flats (53.474°N, 0.155°E). Males in the study area were
152 identified daily via unique pelage markings or *post-hoc* from high resolution pictures taken with a
153 Canon EOS 30D or 40D with a 100-400mm lens (Twiss et al. 1994, Bishop et al. 2014) at distances
154 ranging from 10 – 180 m, yielding a total of 183 males identified in 2011 and 140 males in 2012.

155 Estimated visitation numbers for Donna Nook were provided by the Lincolnshire Wildlife
156 Trust (*personal correspondence*: R. Lidstone-Scott). This included the number of visitors per day on
157 the weekend and a total for visitors over the 5 consecutive weekdays in 2011 and 2012, and the total
158 number of visitors each year since 1993. Differences in weekend visitor attendance between the two
159 years of the present study were tested for using a t-test and differences in total weekday visitors per
160 week across years were compared using a Mann-Whitney U test due to small samples sizes.

161 ***Male activity budgets***

162 An ethogram was generated to allow comparisons between this study and previously
163 conducted behavioural assessments of male grey seals (Table 1S: Boness & James 1979, Anderson &
164 Fedak 1985, Twiss 1991, Lawson 1993, Twiss et al. 1998). The primary observer conducted
165 instantaneous scan sampling of all identified males at five minute intervals while in the field (Altmann
166 1974, Twiss 1991). The order in which males had their behaviours recorded was consistent between
167 scans. Although throughout the season a range of 5-20 males could be sampled at a time, even when
168 peak numbers were scanned, the process of recording all males' behaviours took less than 1min (mean

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= 50s). Both of these considerations ensured that the interval between any given male's samples was consistent at 5min. Activity budgets were then calculated from the scan samples to quantify the proportion of time each male spent in the distinct behavioural categories; in particular, time spent Alert (Table 1S). Some specific behaviours, such as attempted copulation, comprise a small percentage of the total activity budget and are not as informative for discerning potential effects of disturbance. Therefore, for this study some behaviours were combined in order to investigate the percentage of time spent in the broad behavioural categories of Non-Active (Rest + Alert) and Active (all other behaviours). The time spent in Aggression and Reproductive activities was also calculated as the combined time spent in specific behaviours (as noted in Table 1S).

Many males were only scanned for brief periods or for a single day, and over the course of the season there was considerable turnover of males in the study area. To restrict the potential for these records to skew overall averages, previous studies have calculated activity budgets only for individuals that exceed a threshold number of scans; Twiss (1991) used a cut-off of 180 scans while Culloch (2012) used a cut-off of 200 scans. We selected to calculate the activity budgets for males which had >200 scan records as this represented approximately 2 days of observations. Within the spectrum of male attendance behaviour on breeding colonies, these males would be classified as 'Tenured' (Boness 1984, Twiss 1991). Raw values for Sable Island and North Rona activity budgets were provided by SDT from the 1988-1989 seasons on North Rona and 1990 season on Sable Island (Twiss 1991). Due to a geographically isolated 'Yodel' behaviour at Sable Island, 'Non-Active' at this colony was comprised of Rest + Alert + Yodel + Drink + Eat Snow (Twiss 1991). All other behavioural categories were similar to those used at Donna Nook. We acknowledge the use of these datasets might introduce observer biases between the North Rona/Sable Island data and the Donna Nook data. However, differences should be negligible since the observer at Donna Nook was trained by the observer from Twiss (1991), and all data were analysed at a relatively coarse behavioural scale.

The arcsine transformation for proportional data has been criticized for ecological data (Warton & Hui 2011). Therefore, we tested for differences in average activity budgets for behaviours between years within Donna Nook (Total N =118, ID N = 95 (2011 N = 61 males; 2012 N = 57 males)) using generalized linear mixed-effects models with data logit-transformed (Warton & Hui

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2011). ID was included as a random effect to account for pseudoreplication of some individuals across both years. The response variables were the proportion of time males spent in the broad behavioural categories of Non-Active, Alert, Rest, Aggression, and Locomotion, while the predictor variable was Year. Since some males spent 0% of their time in Aggression, to allow for logit-transformation, male activity budgets for this behavioural category were shifted, by adding the minimum, non-zero value for time spent in aggression to all data-points prior to transformation (Warton & Hui 2011). This was also done for Locomotion for the same reasons.

A similar analysis was then conducted to test for differences in activity budgets between breeding colonies (Total N = 211, ID N = 171 (Donna Nook N = 95 males, North Rona N = 56 males, Sable Island N = 20 males)) with models run to compare each of the above behavioural categories against the predictor variable of Colony. ID was again included as a random factor. Best models were selected based on AIC minimization following Richards' (2008) criteria, in which the model with the lowest ΔAIC is the best model, and all models which are not more complex versions of better models, and have ΔAIC < 6 are also retained. All analyses were carried out in R 2.13.1 (R Core Development Team 2011) with the lme4 package (Bates et al. 2011).

RESULTS

Anthropogenic presence at Donna Nook

Lincolnshire Wildlife Trust has monitored the total visitor numbers at Donna Nook since 1993 and their data shows a general increasing trend through 2006, with stabilisation and some yearly fluctuations in the subsequent years (Fig 2). For the two years of the present study, the tourist visitation patterns exhibited variability within and between seasons with the highest weekend visitation numbers in 2011 (t = 1.95, df =17.64, P = 0.03). Weekend visitation in 2011 averaged 3559 (± 591 SE) visitors per day during peak season (Nov 3 – Dec 10), while attendance averaged 2175 (± 392 SE) per day during the same period in 2012 (Fig 3a). The average total number of weekday visitors (summed across 5 weekdays) did not differ between years (U = 23, P = 0.42; Fig 3b). Aerial military training activities occurred during 50% of weekdays in 2011 and 83% of weekdays in 2012.

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Activity budgets

Activity budgets for males at Donna Nook were generally consistent between seasons and demonstrated considerable similarities in comparison to other colonies (Table 1). At Donna Nook, activity budgets across years seemed relatively stable, and Year was not retained as a significant predictor in the models examining differences in activity budgets for time spent in Locomotion, Aggression, Alert, Rest or Non-Active ($\Delta AIC_{null} = 0$ for all models, Table 1). Across colonies, when examining the overall Non-Active (Rest + Alert) activity budgets, Colony was not retained as a predictor variable ($\Delta AIC_{colony} = 9.1$, $\Delta AIC_{null} = 0$); although, males from Sable Island spent a slightly reduced amount of time in Non-Active behaviours (Table 1, Fig 4). Donna Nook males had higher percentages of time spent in aggression than those at North Rona, but spent a similar amount of time in aggression compared to males on Sable Island (Table 1), and in the model, Colony was retained as a significant variable for explaining the differences in the time spent in Aggression ($\Delta AIC_{colony} = 0$, $\Delta AIC_{null} = 10.33$). There was no difference in time spent in locomotion between colonies ($\Delta AIC_{colony} = 3.11$, $\Delta AIC_{null} = 0$). Lastly, males spent more time resting at Donna Nook than at either of the other two colonies (Table 1) and males at Donna Nook spent the least amount of time Alert of the three colonies (Table 1, Fig 5). Both of these patterns were supported by the retention of Colony in the best models for Rest ($\Delta AIC_{colony} = 0$, $\Delta AIC_{null} = 27.04$) and Alert ($\Delta AIC_{colony} = 0$, $\Delta AIC_{null} = 43.0$).

DISCUSSION

Across three breeding colonies, we found no behavioural evidence of increases in anti-predator, vigilance or movement behaviours by breeding male grey seals exposed to human activities, relative to males at non-disturbed colonies, and overall males exhibited similar time budgets for Non-Active behaviours. Rates of active behaviours such as aggression, attempted copulations and locomotion can reflect trade-offs between fitness and conservation of energy for capital breeders. For grey seals, these behaviours have been shown to vary across environmental gradients such as topography (Anderson & Harwood 1985, Twiss 1991), sex-ratio (Twiss et al. 1998) or weather patterns (Twiss et al. 2006). However, the consistency across colonies we found for the time males spent in Non-Active behaviours suggests strong selection pressures for overarching conservation of

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energy across the geographic range, across a variety of topographies, and in the presence or absence of human disturbance. Males in other highly polygynous species such as the South American sea lion, *Otaria byronia*, (Pavez et al. 2014) and the California sea lion, *Zalophus californianus* (Holcomb et al. 2009) have also shown reduced responses to disturbance relative to females. Selection for this lack of a behavioural response is likely driven by the increased mating success of males who maintain their position amongst groups of females for the longest time; either through greater initial energy stores (mass) or by reduced energy spent on active behaviours (Twiss 1991, Lidgard et al. 2001, Lidgard et al. 2005).

Previous studies have found little evidence of military activities or helicopters disturbing grey seal behaviour (Perry et al. 2002, Southwell 2005), but there is a lack of consensus on whether or not tourism activities, either on land or sea, negatively impact pinniped behaviours (Engelhard et al. 2002, Curtin et al. 2009, Holcomb et al. 2009, Pavez et al. 2011, Hoover-Miller et al. 2013, Le Boeuf & Campagna 2013, Cowling et al. 2014, Granquist & Sigurjonsdottir 2014, Pavez et al. 2014). Studies which note negative effects at specific locations (Curtin et al. 2009, Pavez et al. 2011, Granquist & Sigurjonsdottir 2014, Pavez et al. 2014) are often isolated or may not consider acute responses in relation to the broader behavioural ecology and evolution of the species. For example, Christiansen et al. (2013) found that the presence of whale-watching vessels did reduce the amount of time minke whales, *Balaenoptera acutorostrata*, spent foraging. However, when considering the temporal and spatial rates of individuals' exposure over an entire season, there appeared to be no potential for a population level effect of these acute disturbances (Christiansen et al. 2015). By examining activity budgets of male grey seals across breeding colonies at a coarse, seasonal scale, our results also suggest that while acute responses to tourism disturbances might be occurring, there appear to be no differences in average time spent Non-Active for males across breeding colonies.

Although the intensity of human activities differed between years for wildlife tourism and military actions at Donna Nook, there were no corresponding between-year differences in any behavioural categories and the time males spent Alert in both years was lower than at the undisturbed colonies. In comparison, for harbour seals, increases in Alert behaviours were positively correlated with the number of wildlife viewers during the breeding season (Granquist & Sigurjonsdottir 2014)

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and males both increased vigilance behaviours and had some indication of increased heart-rate following sonic booms during the non-breeding season (Perry et al. 2002). Harbour seals do not hold terrestrial territories during the breeding season (van Parijs et al. 2000), and are not sexually size-dimorphic (González-Suárez & Cassini 2014), suggesting that the selection pressures for conservation of energy in this species are potentially not as strong as those for male grey seals both during and outside of breeding seasons. These comparisons suggest that specific selection pressures, life-histories, and ecological constraints should be considered if attempting to infer management strategies for disturbance, even across closely related species.

While we have demonstrated that male grey seals, like other male pinnipeds, appear to have strong selection pressures driving their activity budgets during the temporally discrete breeding season; this study was not able to discern the mechanism driving this pattern directly. The apparent lack of effect of human activities on Non-Active or Alert behaviours in other studies has been attributed to: (1) individuals not exhibiting any anti-predator response in respects to human activities (Cobley & Shears 1999, Holcomb et al. 2009, Pavez et al. 2014), (2) differences in tolerance thresholds resulting in intolerant individuals being displaced (Bejder et al. 2009), or (3) individuals exhibiting initial acute responses to anthropogenic presence but subsequently habituating (Bright et al. 2003, Villanueva et al. 2012, Côté et al. 2013, Le Boeuf & Campagna 2013). None of these mechanisms are mutually exclusive, and we will consider each scenario in terms of the species' behavioural ecology and potential management implications.

Many of the species which exhibit increases in vigilance are social species, with considerable selection for anti-predator behaviours (Roberts 1996, Duchesne et al. 2000, Lusseau 2003, Côté et al. 2013). The last potential terrestrial predator of grey seals in the UK, the wolf, *Canis lupus*, was extirpated around 1770 (Nilsen et al. 2007). Additionally, since the Conservation of Seals Act of 1970, human culling of grey seals in England can only occur under licence, further reducing any potential for males to experience perceived risks while hauled out. The Donna Nook colony formed in the 1980s and did not begin to grow rapidly until 1992 (Duck & Morris 2010, pers. corr RLS). Tourist visitation and the population of seals both gradually increased through 2006, but direct access to the

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colony was limited by a fence since 1997 and further limited by a second fence layer in 2007 (pers. corr RLS). Therefore, it is possible that current, reproductively active adult male seals (typically aged 8-20 years, Twiss 1991) at Donna Nook have not experienced negative exposure that would have led individuals to associate human presence with a threat. Gentoo penguin (*Pygoscelis papua*) colonies in Antarctica have little to no history of land predators and do not exhibit behavioural changes in response to human activities (Cobley & Shears 1999). Similarly, a lack of terrestrial predators has also been suggested as a reason male California sea lions do not respond to tourism disturbances (Holcomb et al. 2009). Thus, focusing on the historical evolutionary selection pressures could identify candidate species for future wildlife viewing opportunities, or help avoid species which have been selected for greater anti-predator responses.

Second, a wide range of animals have demonstrated individual differences, but behavioural consistency, in their responses to stimuli (Bell et al. 2009). Male grey seals have demonstrated individual behavioural consistencies in the amount of time they spend Alert (Twiss & Franklin 2010). Twiss et al. (2012) also demonstrated that female grey seals vary in their response to disturbance and either display proactive or reactive behavioural types. The extent of variation in behavioural types in a population could influence responses to disturbance; for example, colonies might be selecting for individuals with specific behavioural types, such as high tolerance to disturbance, and displacing individuals spatially or temporally with lower thresholds (Bejder et al. 2009, Higham & Shelton 2011). The ease with which individuals with lower tolerance thresholds can be temporally or spatially displaced is likely dependent on the topography, available habitat (Bennett et al. 2013), and temporal constraints of key life-history periods. Therefore, population level effects could be masked depending on the spatial or temporal scale of the sample. In the present study, male seals at Donna Nook are not space-limited and large portions of the beach are still available for breeding seals (pers. obs). If males differed in their tolerance to disturbance, displacement might not result in being driven off the colony altogether, as it might at colonies with limited breeding substrate. Instead, less tolerant males might select to occupy more peripheral locations. While we cannot rule out spatial displacement within Donna Nook, it is unlikely to have influenced our results. Male distance from the fence ranged from 10m-350m, and all seals were exposed to the military training exercises.

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Temporal displacement is quite different. Unlike hauling-out behaviours which can be temporally and spatially displaced due to wildlife viewing (Granquist & Sigurjonsdottir 2014), breeding seasons are temporally keyed by females' reproductive cycles, involving the interplay of hormone and environmental cues controlling fertilization, implantation, gestation, parturition and oestrus (Pomeroy et al. 2000).This restricts the effectiveness of any plasticity males can demonstrate in their responses. Therefore, as capital breeders, the temporal constraints of the breeding season, along with the selection pressures for maintaining access to females and for conservation of energy, might be overriding any between-individual differences in tolerance, resulting in the observed lack of differences across colonies during this life history stage.

Finally, habituation to tourism activities has been demonstrated in species such as the dabchick, *Poliocephalus rufopectus* (Bright et al. 2003) and Magellanic penguins, *Spheniscus magellanicus* (Villanueva et al. 2012). The lack of an observed increase in Alert responses at Donna Nook could be due to males responding to protracted exposure by returning to pre-exposure levels. Due to the importance of 'not losing' for male grey seals (Anderson & Fedak 1985), Alert behaviours during the breeding season are likely a mechanism for monitoring threats from competitor males and potential intrusions (Twiss 1991, Lawson 1993). Donna Nook has been exposed to anthropogenic presence since the formation of the colony and initially, visitors were able to access the colony without restriction. During this time, if humans were perceived as potential intrusions into male grey seals' loose spatial territories, it is possible males increased the frequency of Alert behaviours. However, visitor presence has increased over the years simultaneously with the number of seals, potentially leading to a gradual habituation. At an even finer temporal scale, within a breeding season, the number of visitors also gradually increases over time, potentially leading to within-season habituation over the course of a few days (Villanueva et al. 2012).

In this study, only adult, tenured males were included in our selection criteria for observation as these males experience the highest rates of mating success (Twiss 1991, Lidgard et al. 2001, Lidgard et al. 2005). Donna Nook is an expanding colony (Duck & Morris 2010), so it is likely that population growth is a product of both immigration as well as internal growth (with the observed 40% increases, the maximum intrinsic rate is ~12%; *personal communication*, P. Pomeroy). If immigration

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363 is occurring, some males sampled could potentially be non-habituated, but if these newcomer males
364 are younger, or males exhibiting the alternative, transient mating strategy (Boness & James 1979,
365 Lidgard et al. 2001) they might have been excluded based on our sample criteria. Future studies
366 would thus benefit from looking in more detail at these peripheral or newcomer individuals to
367 determine the potential for non-habituated responses to human activities or to monitor the potential
368 occurrence of habituation over time.

369 Habituation in response to human activities has been criticized as a negative effect, as it could
370 potentially reduce the overall fitness of a population by reducing the natural fight-or-flight response,
371 or by promoting further human-wildlife conflict (Bejder et al 2009). Others, however, have argued
372 that in terms of scientific research, habituation to observers for primates or small mammals is
373 considered acceptable (Higham & Shelton 2011). The present study cannot ascertain if males have
374 habituated to tourism at Donna Nook, but the current management of the colony restricts any direct
375 human-seal contact, and the continual population growth at Donna Nook and other mainland colonies
376 in the region suggests that at present, there appears to be no adverse effects on individual fitness or on
377 population growth.

378

379 **Management Implications and Future Work**

380 Legislation, such as the Marine Mammal Protection Act of 1972 (MMPA) in the USA,
381 prohibits disturbance of marine mammals through clauses that define 'harassment' as any act which
382 "has the potential to disturb a marine mammal or marine mammal stock in the wild by causing
383 disruption of behavioural patterns, including, but not limited to, migration, breathing, nursing,
384 breeding, feeding, or sheltering". In the UK, similar laws prohibit intentional harassment or
385 disturbance of pinnipeds at significant haul-out sites (Marine Scotland Act 2010), while others
386 prohibit direct takes of animals through culling or hunting (Conservation of Seals Act 1970). To
387 uphold these legislative directives, managers must first be able to identify when animals enter periods
388 of disturbance. Ecotourism is often argued to be beneficial to wildlife through public education and
389 establishments of wildlife reserves, but it is also criticized as prone to the tragedy of the commons
390 (Heenehan et al. 2014) and is an economy which can result in disturbance and reduced fitness for

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populations of animals (Shackley 1996). Likewise, military training grounds can often provide refuge or habitat for animals (Warren & Büttner 2008) but with potential costs of increased wildlife disturbance (DeRuiter et al. 2013). It is unlikely that either side of the argument is universal and applicable to all species. This study provides evidence that although breeding periods can be energy limited and have often been considered critical times (Hoover-Miller et al. 2013), strong natural or sexual selection pressures during this discrete period can potentially mitigate the pressures to change behaviours across a gradient of anthropogenic exposure in the form of wildlife tourism.

We recognize the specific conditions of our study (*e.g.* we only considered breeding males and not females, pups or subordinate males) but within this framework, we provide evidence suggesting that understanding the selection pressures, spatial and temporal constraints, and life-history of a particular species in question, or sex within a species, is paramount for effective management. Thus, future work in the field of human-wildlife interactions and management will benefit from studies which; (1) are targeted to specific sexes and life history stages to examine potential differences in how selection pressures and responses vary (Cowling et al. 2014), (2) are spatially and temporally explicit across a wide range of exposure levels within and between populations to examine differences in responses to disturbance (Christiansen et al. 2015), (3) incorporate both behavioural and physiological metrics such as heart rate (Lydersen & Kovacs 1995) or stress hormones to examine for 'hidden' effects and individual variation in responses (Villanueva et al. 2012), and (4) use interdisciplinary methods to investigate the efficacy of specific management practices (Le Boeuf & Campagna 2013). Further consideration of these questions will work towards improving our knowledge of how human presence functions as part of the ecological and selection pressures driving species.

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References

Altmann J. 1974. Observational study of behaviour: sampling methods. Behaviour. 49: 227-265.

Anderson SS, Burton RW, Summers CF. 1975. Behaviour of grey seals (*Halichoerus grypus*) during a breeding season at North Rona. J Zool. 177:179-195.

Anderson SS and Fedak MA. 1985. Grey seal males: energetic and behavioural links between size and sexual success. Anim Behav. 33:829-838.

Anderson SS and Harwood J. 1985. Time budgets and topography: how energy reserves and terrain determine the breeding behaviour of grey seals. Anim Behav. 33:1343-1348.

Ballantyne R, Packer J, Hughes K. 2009. Tourists' support for conservation messages and sustainable management practices in wildlife tourism experiences. Tourism Manage. 30:658-664.

Barker J, Seymour A, Mowat S, Debney A. 2014. Thames harbour seal conservation project. Report for the UK & Europe Conservation Programme, Zoological Society of London.

Bates D, Maechler M, Bolker B. 2011. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42. http://CRAN.R-project.org/package=lme4.

Bejder L, Samuels A, Whitehead H, Finn H, Allen S. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Mar Ecol Prog Ser. 395:177-185.

Bell AM, Hankinson SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. Anim Behav. 77:771-783.

Bennett VJ, Quinn VS, Zollner PA. 2013. Exploring the implications of recreational disturbance of an endangered butterfly using a novel modelling approach. Biodivers Conserv. 22:1783-1798.

Bishop AB, Lidstone-Scott R, Pomeroy PP, Twiss SD. 2014. Body Slap: An innovative aggressive display by breeding male gray seals (*Halichoerus grypus*). Mar Mammal Sci.30:579-593. DOI: 10.1111/mms.12059.

Boness DJ. 1984. Activity budget of male gray seals, *Halichoerus grypus*. J Mammal. 65:291-297.

Boness DJ and James H.1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. J Zool. 188:477–500.

Bright A, Reynolds GR, Innes J, Waas JR. 2003. Effects of motorised boat passes on the time budgets of New Zealand dabchick, *Poliocephalus rufopectus*. Wildlife Res. 30:273-244.

Catlin J, Jones R, and Jones T. 2011. Revisiting Duffus and Dearden's wildlife tourism framework. Biol Conserv. 144:1537-1544.

457 Christiansen F, Rasmussen M, Lusseau D. 2013. Whale watching disrupts feeding activities of minke
458 whales on a feeding ground. Mar Ecol Prog Ser. 478:239-251.
459
460 Christiansen F, Bertulli CG, Rasmussen MH, Lusseau D. 2015. Estimating cumulative exposure of
461 wildlife to non-lethal disturbance using spatially explicit capture-recapture models. J Wildl
462 Manage. 79: 311-324.
463
464 Cobley ND, and Shears JR. 1999. Breeding performance of Gentoo penguins (*Pygoscelis papua*) at a
465 colony exposed to high levels of human disturbance. Polar Biol. 21:355-360.
466
467 Conservation of Seals Act 1970. http://www.legislation.gov.uk/ukpga/1970/30

468 Converse SJ, Iverson JB, Savidge JA. 2005. Demographics of an ornate box turtle population
469 experiencing minimal human-induced disturbances. Ecol Appl. 15:2171–2179.

470 Côté SD, Hamel S, St-Louis A, Mainguy J. 2013. Do mountain goats habituate to helicopter
471 disturbance? J Wildlife Manage. 77: 1244-1248.

472 Cowling M, Kirkwood R, Boren L, Sutherland D. 2014. The effects of vessel approaches on the New
473 Zealand fur seal (*Arctocephalus forsteri*) in the Bay of Plenty, New Zealand. Mar Mammal
474 Sci. DOI: 10.1111/mms.12171

475 Culloch R. 2012.The application of modern statistical approaches to identify consistent individual
476 differences in the behaviour of wild postpartum female grey seals (*Halichoerus grypus*). PhD
477 Thesis. Durham University, Durham, UK. 446pp.

478 Curtin S. 2013. Lessons from Scotland: British wildlife tourism demand, product development and
479 destination management. Journal of Destination Marketing and Management. 2:196-211.

480 Curtin S, Richards S, Westcott S. 2009. Tourism and grey seals in south Devon: management
481 strategies, voluntary controls and tourists' perceptions of disturbance. Current Issues in
482 Tourism. 12:59-81.

483 DeRuiter SL, Southall BL, Calambokidis J, Zimmer WM, Sadykova D, Falcone EA, Tyack PL. 2013.
484 First direct measurements of behavioural responses by Cuvier's beaked whales to mid-
485 frequency active sonar. Biol Lett. 9: 20130223.

486 Duchesne M, Côté SD, Barrette C. 2000. Responses of woodland caribou to winter ecotourism in the
487 Charlevoix Biosphere Reserve, Canada. Biol Conserv. 96:311-317.

488 Duck CD and Morris CD. 2010. Grey seal pup production in Britain in 2009. Special Committee on
489 Seals briefing paper 10/1. Unpublished. (Available from: NERC Sea Mammal Research Unit,
490 Scottish Oceans Institute, University of St. Andrews, St. Andrews, KY16 8LB, UK.)

491 Duffus DA and Dearden P. 1990. Non-consumptive wildlife-oriented recreation: A conceptual
492 framework. Biol Conserv. 53:213-231.

493 Englehard GH, Baarspul ANJ, Broekman M, Creuwels JCS, Reijnders PJH. 2002. Human
494 disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant
495 seal (*Mirounga leonina*) population. Can J Zool. 80:1876-1886.

496 Frid A and Dill L. 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv Ecol.
497 6:11, [online] URL: http://www.consecol.org/vol6/iss1/art11/

498 Granquist SM and Sigurjonsdottir H. 2014. The effect of land based seal watching tourism on the
499 haul-out behaviour of harbour seals (*Phoca vitulina*) in Iceland. Appl Anim Behav Sci.
500 156:85-93.

González-Suárez M and Cassini MH. 2014. Variance in male reproductive success and sexual size dimorphism in pinnipeds: testing an assumption of sexual selection theory. Mammal Review, 44: 88-93.

Hardiman N and Burgin S. 2010. Recreational impacts on the fauna of Australian coastal marine ecosystems. J Environ Manage. 91:2096-2108.

Heenehan H, Basurto X, Bejder L, Tyne J, Higham JE, Johnston DW. 2014. Using Ostrom's common-pool resource theory to build toward an integrated ecosystem-based sustainable cetacean tourism system in Hawaii. J Sustainable Tour. (ahead-of-print), 1-21.

Higham JES and Shelton EJ. 2011. Tourism and wildlife habituation: Reduced population fitness or cessation of impact? Tourism Manage. 32: 1290-1298.

Holcomb K, Young JK, Gerber LR. 2009. The influence of human disturbance on California sea lions during the breeding season. Anim Cons. 12: 592-598.

Hoover-Miller A, Bishop A, Prewitt J, Conlon S, Jezierski C, Armato P. 2013. Efficacy of voluntary mitigation in reducing harbour seal disturbance. J Wildlife Manage. 77:689-700

Jett J, Thapa B, Swett R. 2013. Boater speed compliance in manatee zones: examining a proposed predictive model. Society and Natural Resources: An international journal, 26:95-104.

Lawson JM.1993. A descriptive and quantitative comparison of the communication of gray seals, Halichoerus grypus, at three sites in the North Atlantic Ocean. Ph.D. thesis, Memorial University, St. John's, Newfoundland, Canada. 330 pp. Available at http://collections.mun.ca/PDFs/theses/Lawson_JohnWarren2.pdf.

Le Boeuf BJ and Campagna C. 2013. Wildlife viewing spectacles: best practices from elephant seal (*Mirounga* sp.) colonies. Aquat Mamm. 39: 132-146.

Lewis TM and Mathews EA. 2000. Effects of human visitors on the behavior of harbor seals (Phoca vitulina richardsi) at McBride Glacier Fjord, Glacier Bay National Park. Final Report to Glacier Bay National Park Management Division. P.O. Box 140, Gustavus Alaska 99826.

Lewison RL, et al. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. PNAS 11:5271-5276.

Lidgard DC, Boness DJ, Bowen WD. 2001. A novel mobile approach to investigating mating tactics in male grey seals (*Halichoerus grypus*). J Zool. 255:313-320.

Lidgard DC, Boness DJ, Bowen WD, McMillan JI, Fleischer RC. 2004. The rate of fertilization in male mating tactics of the polygynous grey seal. Mol. Ecol. 13:3543-3548.

Lusseau D. 2003. Effects of tour boats on the behaviour of bottlenose dolphins: using markov chains to model anthropogenic impacts. Conserv Biol. 17:1785-1793.

Lydersen C and Kovacs KM. 1995. Paralysis as a defence response to threatening stimuli in harp seals (*Phoca groenlandica*). Can J Zool. 73:486-492.

Marine Mammal Protection Act, 1972. 16 US 1361. http://www.nmfs.noaa.gov/pr/laws/mmpa/text.htm

Marine Scotland Act 2010. http://www.legislation.gov.uk/asp/2010/5/pdfs/asp_20100005_en.pdf

DRAFT

546 Mustika PLK, Birtles A, Everingham Y, Marsh H. 2013. The human dimensions of wildlife tourism
547 in a developing country: watching spinner dolphins at Lovina, Bali, Indonesia. J Sustain Tour.
548 21:229-251.

549 NEFSC. 2010. Grey seal (*Halichoerus grypus grypus*): Western North Atlantic Stock.
550 http://www.nefsc.noaa.gov/publications/tm/tm219/184_GRSE.pdf

551 Nilsen EB, Milner-Gulland EJ, Schofield L, Mysterud A, Stenseth NC, Coulson T. 2007. Wolf
552 reintroduction to Scotland: public attitudes and consequences for red deer management. Proc.
553 R. Soc. B. 274:995-1003.

554 Pavez G, Muñoz L, Inostroza P, Sepúlveda M. 2011. Behavioral response of South American sea lion
555 *Otaria flavescens* to tourist disturbance during the breeding season. Rev. Biol. Mar. oceanogr.
556 46:135-140.

557 Pavez G, Muñoz L, Barilari F, Sepúlveda M. 2014. Variation in behavioural responses of the South
558 American sea lion to tourism: implications for tourism management. Mar Mamm Sci. DOI:
559 10.1111/mms.12159.

560 Perry EA, Boness DJ, Insley SJ. 2002. Effects of sonic booms on breeding gray seals and harbour
561 seals on Sable Island, Canada. J Acoust Soc Am. 111:599-609.

562 Pirotta E, Brookes KL, Graham IM, Thompson PM. 2014. Variation in harbour porpoise activity in
563 response to seismic survey noise. Biol Lett. 10: 20131090. DOI:
564 http://dx.doi.org/10.1098/rsbl.2013.109

565 Pomeroy PP, Anderson SS, Twiss SD, McConnell BJ. 1994. Dispersion and site fidelity of breeding
566 female grey seals (*Halichoerus grypus*) on North Rona, Scotland. J Zool. 233:429-447.

567 Pomeroy PP, Twiss SD, Redman P. 2000. Philopatry, site fidelity and local kin associations within
568 grey seal breeding colonies. Ethology. 10**:** 899-919.

569 Richards SA. 2008 Dealing with overdispersed count data in applied ecology. J Appl Ecol. 45:218-
570 227.

571 Roberts G. 1996. Why individual vigilance declines as group size increases. Anim Behav. 51:1077-
572 1086.

573 SGSR. 2010. The economic impact of wildlife tourism in Scotland.
574 http://www.scotland.gov.uk/Resource/Doc/311951/0098489.pdf

575 Shackley M. 1996. Wildlife tourism. International Thomson Business Press.
576
577 Skeate ER, Perrow MR, Gilroy JJ. 2012. Likely effects of construction of Scroby Sands offshore
578 windfarm on a mixed population of harbour *Phoca vitulina* and grey *Halichoerus grypus*
579 seals. Mar Pollut Bull. 64:872-881.
580
581 Southwell C. 2005. Response behaviour of seals and penguins to helicopter surveys over the pack ice
582 off East Antarctica. Antarct Sci. 17: 328-334.
583
584 Stevens MA and Boness DJ. 2003. Influences of habitat features and human disturbance on use of
585 breeding sites by a declining population of southern fur seals (*Arctocephalus australis*). J
586 Zool. 260:145-152.
587
588 Strong P and Morris SR. 2010. Grey seal (*Halichoerus grypus*) disturbance, ecotourism and the
589 Pembrokeshire Marine Code around Ramsey Island. J Ecotourism. 9:117-132.

DRAFT

Suryan RM and Harvey JT. 1999. Variability in reactions of the Pacific harbor seal (*Phoca vitulina richardsi*) to disturbance. Fish Bull. 97: 332-339.

Treves A and Karnth KU. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. Conserv Biol, 17: 1491–1499.

Twiss SD. 1991. Behavioural and energetic determinants of individual mating and success in male grey seals (*Halichoerus grypus*). Ph.D. thesis, University of Glasgow, Glasgow, U.K. 337 pp.

Twiss SD, Pomeroy PP, Anderson SS. 1994. Dispersion and site fidelity of breeding male grey seals (*Halichoerus grypus*) on North Rona, Scotland. J Zool 233:683–693.

Twiss SD, Anderson SS, Monaghan P. 1998. Limited intra-specific variation in male grey seal (*Halichoerus grypus*) dominance relationships in relation to variation in male mating success and female availability. J Zool. 246:259–267.

Twiss SD, Poland VF, Graves JA, Pomeroy PP. 2006. Finding fathers: spatio-temporal analysis of paternity assignment in grey seals (*Halichoerus grypus*). Mol Ecol. 15:1939-1953.

Twiss SD and Franklin J. 2010. Individually consistent behavioural patterns in wild, breeding male grey seals (*Halichoerus grypus*). Aquat Mamm. 36:234-238.

Twiss SD, Cairns C, Culloch RM, Richards SA, Pomeroy PP. 2012. Variation in female grey seal (*Halichoerus grypus*) reproductive behaviour correlates to proactive-reactive behavioural types. PLoS ONE 7(11): e49598. doi:10.1371/journal.pone.0049598

USA Census 2012, http://stateofthecoast.noaa.gov/population/welcome.html

van Parijs SM, Hastie GH, and Thompson PH. 2000. Individual and geographical variation in display behaviour of male harbour seals in Scotland. Anim. Behav, 59:559-568.

Velando A and Munilla I. 2011. Disturbance to a foraging seabird by sea-based tourism: implications for reserve management in marine protected areas. Biol Conserv. 144:1167-1174.

Villanueva C, Walker BG, Bertellotti M. 2012. A matter of history: effects of tourism on physiology, behaviour and breeding parameters in Magellanic Penguins (*Spheniscus magellanicus*) at two colonies in Argentina. J Ornithol. 153:219-228.

Warren SD and Büttner R. 2008. Relationship of endangered amphibians to landscape disturbance. J Wildlife Manage. 72:738-744.

Warton DI and Hui FKC. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology. 92:3-10.

Williams R, Lusseau D, Hammond PS. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biol. Conserv. 133:301-311.

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628 **Figure Captions**

629 **Figure 1**: *Halichoerus grypus.* Locations of grey seal breeding colonies in the North Atlantic with
630 published datasets available for male activity budgets. Data from Sable Island (Canada) and North
631 Rona (Scotland) were collected by Twiss (1991). Data from Donna Nook was collected for the
632 present study.
633
634 **Figure 2:** The total visitors at Donna Nook during the breeding season (Nov and Dec) each year.
635 Annotations indicate timing of events which correlate with dramatic increases or decreases in
636 visitation numbers (data and annotations from: Lincolnshire Wildlife Trust, Rob Lidstone-Scott).
637
638 **Figure 3:** The number of visitors at Donna Nook on individual weekend days only for 2011and 2012
639 at the PUB site (a) and weekday totals (total number of visitors across 5 week days) (b).
640
641 **Figure 4:** *Halichoerus grypus.* The median percentage of time spent in Non-Active behaviours at
642 each of the three colonies (Donna Nook = DN11 & DN12 (in 2011 and 2012); North Rona = NR88 &
643 NR89 (in 1988 and 1989); Sable Island = SI90 (in 1990)). Boxes represent the interquartile range
644 around the median (dark line) with notches displaying the 95% confidence interval around the
645 median. Whiskers represent the 75^{th} and 25^{th} percentile respectively. Circles outside of whiskers
646 represent possible outlies.
647
648 **Figure 5:** *Halichoerus grypus.* The median percentage of time spent Alert at each of the three
649 colonies (Donna Nook = DN11 & DN12 (in 2011 and 2012); North Rona = NR88 & NR89 (in 1988
650 and 1989); Sable Island = SI90 (in 1990)). Boxes represent the interquartile range around the median
651 (dark line) with notches displaying the 95% confidence interval around the median. Whiskers
652 represent the 75^{th} and 25^{th} percentile respectively. Circles outside of whiskers represent possible
653 outlies.
654
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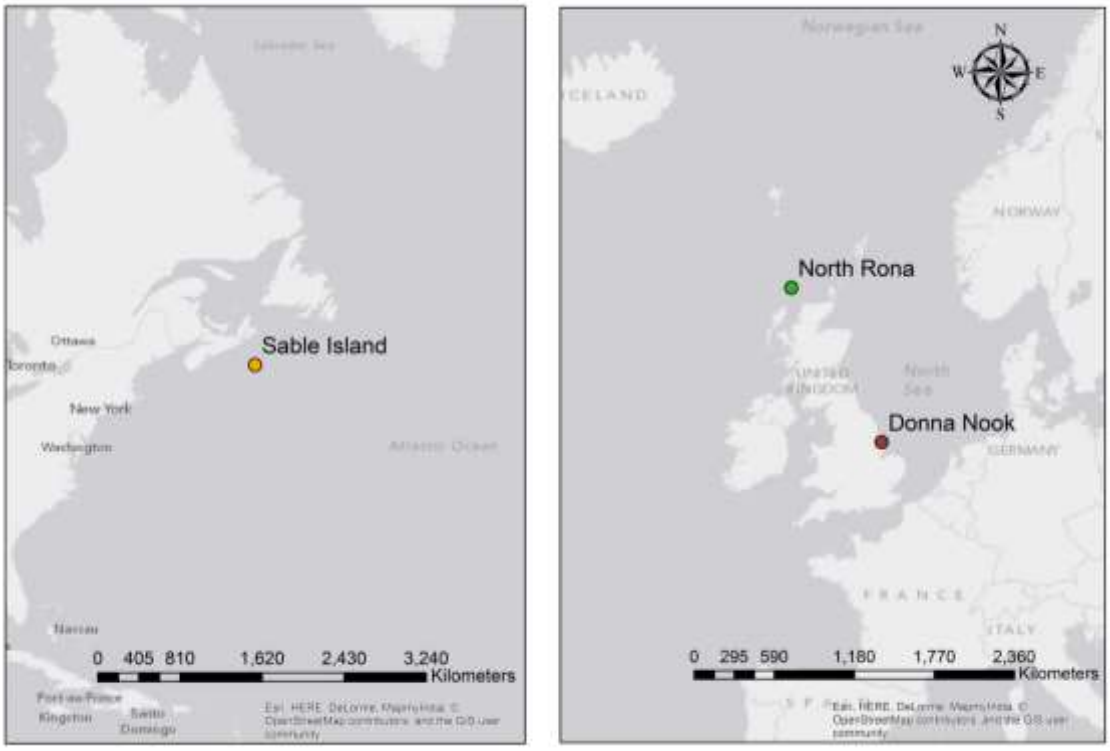

656 **Figure 1**

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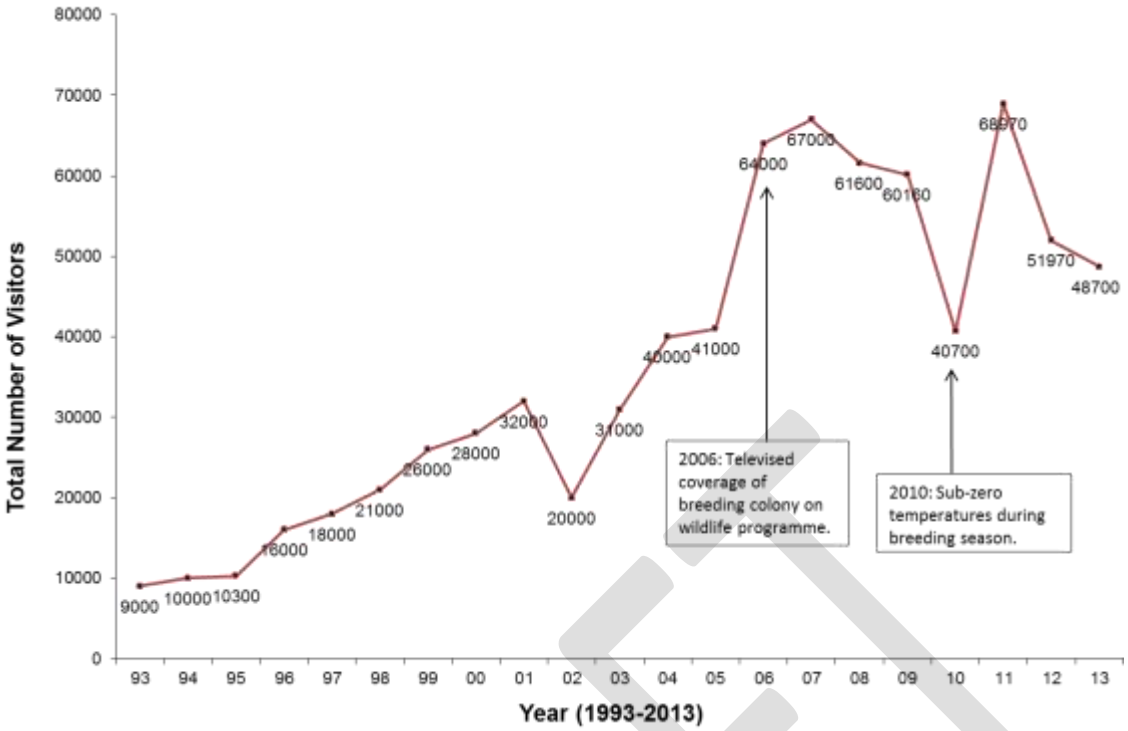


Figure 2

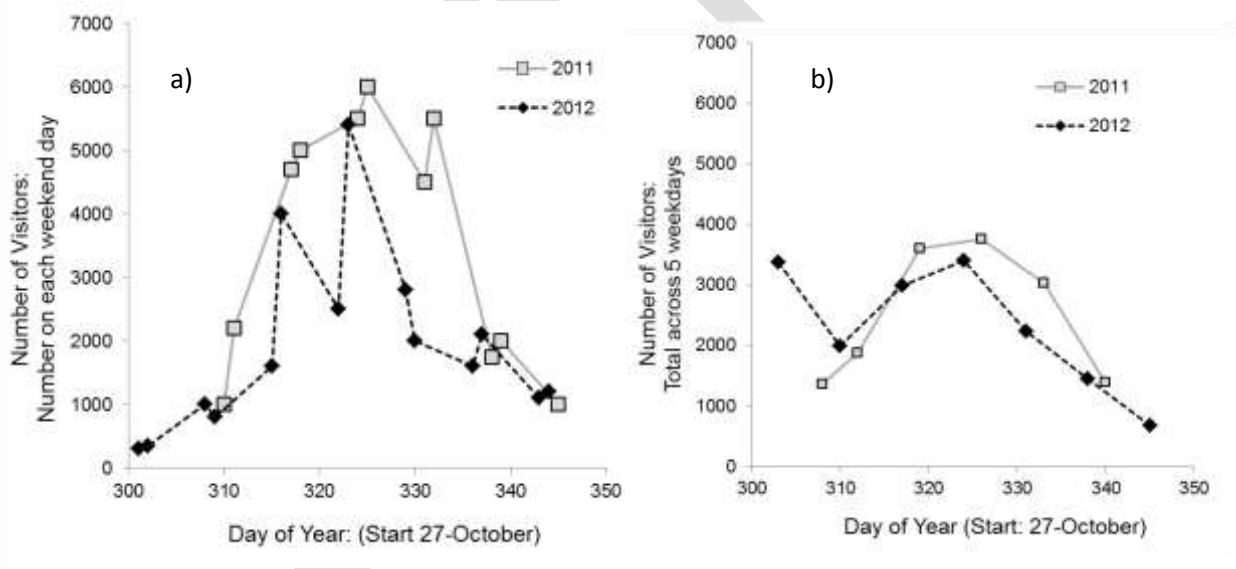
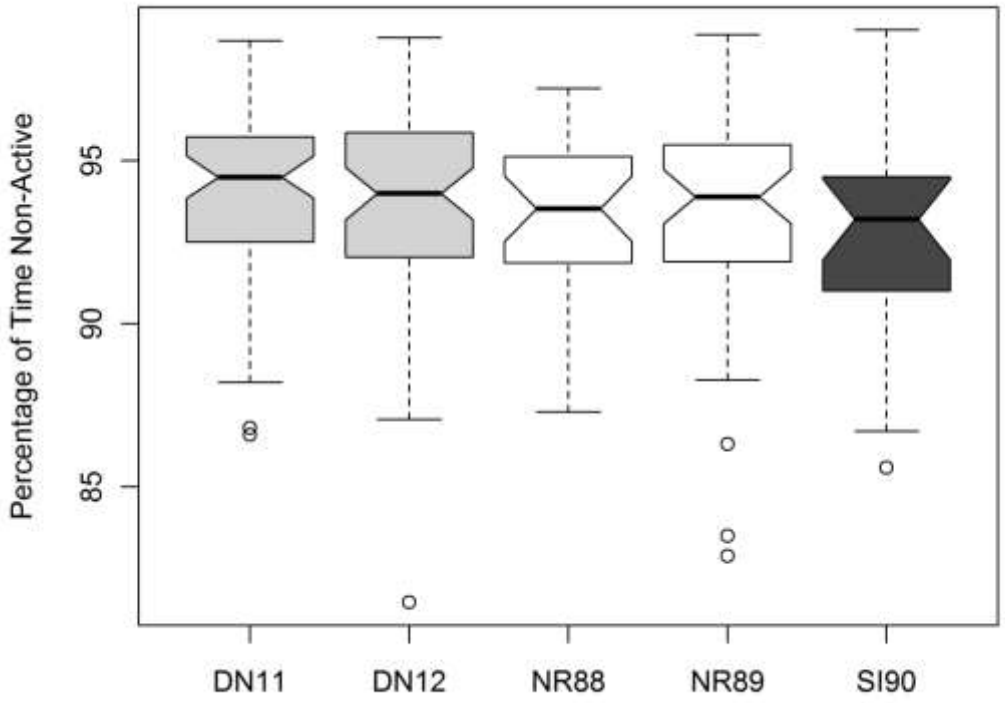
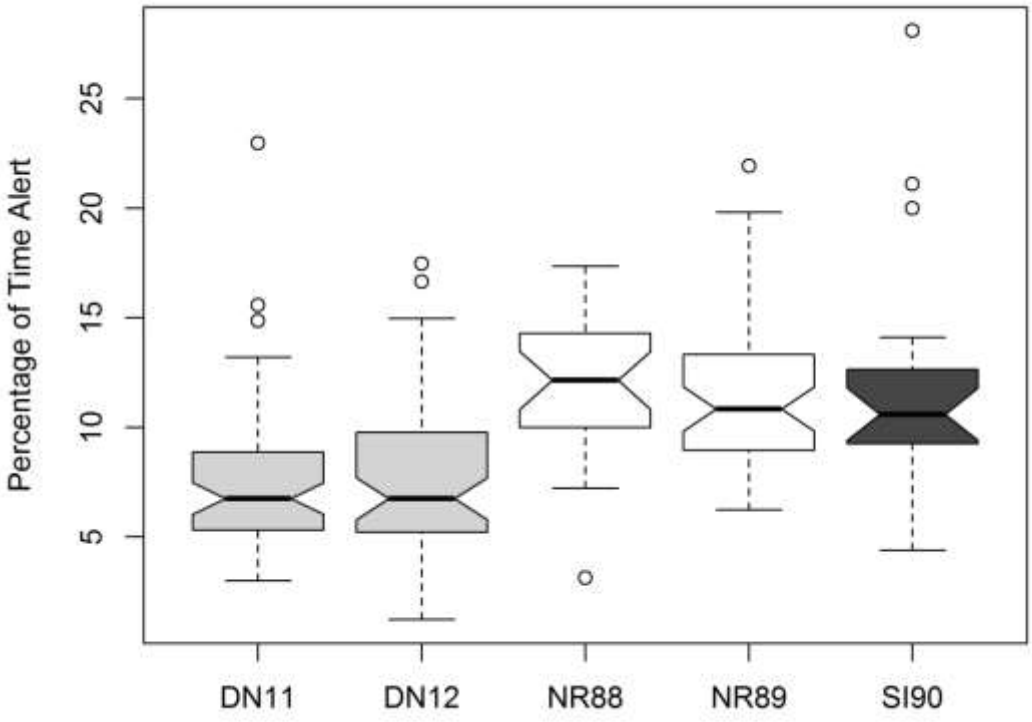


Figure 3



671 **Figure 4**



672
673 **Figure 5**

674 **Table 1:** Activity budgets for males at Donna Nook and comparison colonies (±SE); Percentage of
675 time spent in each activity is the mean across all males with ≥200 scans (or ≥180 scans for North
676 Rona and Sable Island*).

	2011 (*n* = 61)	2012 (*n* = 57)	DN (*n =118)*	NR (*n = 73)* *	SI (*n* = 20) *
§Rest	86.48 (0.62)	85.63 (0.76)	86.07 (0.45)	81.55 (0.63)	79.76 (2.02)
§Alert	7.54 (0.45)	7.88 (0.47)	7.70 (0.33)	11.77 (0.42)	11.76 (1.27)
Locomotion	1.47 (0.13)	1.33 (0.12)	1.40 (0.09)	1.70 (0.12)	1.83 (0.26)
§ Yodel	--	--	--	--	0.72 (0.33)
†Approach Female	0.09 (0.02)	0.00 (0.00)	0.09 (0.02)	0.36 (0.04)	0.26 (0.08)
†Attempted Copulation	0.53 (0.07)	0.49 (0.07)	0.52 (0.05)	0.89 (0.10)	0.51 (0.14)
†Copulation	0.77 (0.13)	0.91 (0.12)	0.84 (0.08)	1.32 (0.14)	0.90 (0.31)
†Non-Ag Flip	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.003)	0.01 (0.005)
‡α Aggression to Females	0.08 (0.02)	0.65 (0.08)	0.35 (0.05)	--	--
‡Non-Contact	2.87 (0.27)	2.58 (0.18)	2.73 (0.13)	2.09 (0.16)	3.31 (0.37)
‡Contact	0.16 (0.03)	0.12 (0.06)	0.14 (0.02)	0.41 (0.06)	0.24 (0.10)
Reproductive	1.39 (0.19)	1.82 (0.27)	1.59 (0.16)	2.48 (0.20)	1.68 (0.45)
Aggressive	3.11 (0.21)	3.34 (0.17)	3.21 (0.14)	2.27 (0.17)	3.55 (0.40)
Non-Active	94.02 (0.33)	93.51 (0.39)	93.78 (0.25)	93.55 (0.36)	92.91 (0.72)
Active	5.98 (0.33)	6.48 (0.39)	6.22 (0.25)	6.44 (0.36)	7.05 (0.72)

**NR = North Rona Colony 1988 & 1989; SI = Sable Island 1990 (Twiss 1991).*
§ = *Behaviours included in 'Non-Active'*
† = *Behaviours included in 'Reproductive'*
‡ = *Behaviours included in 'Aggressive (male)'*
α = Aggression to females consisted of any 'Aggressive' behaviour directed at a female

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679 **Supplementary**

680 **Table 1S:** Ethogram of behaviours used during scan-sampling and for calculating activity budgets of
681 males at Donna Nook. For additional behaviours see: Twiss 1991 and Lawson 1993.

Aggressive Behaviours	
Approach male	Focal male moves directly towards another male (Bishop et al. 2014).
Open Mouth Threat	This is a threat display which consists of a male opening his mouth to a wide gape directed at opponent with no vocalization or contact with conspecific (Twiss 1991, Lawson 1993, Bishop et al. 2014).
Aggressive Flippering	The behaviour involves a male vigorously waving his fore-flippers and/or slapping his own sides in a clearly aggressive manner.
Lunge	An attempt to bite without making contact.
Bite	A singular bite or contact made through a lunge. This behaviour is sometimes associated with a vigorous shaking of the head laterally while maintaining grasp of opponent. Subcategory of this behaviour is Bite Hind Flippers (BHF) where male grasps opponents' hind-flippers or tail with his mouth.
Fight or Contact AI	The segment of an aggressive interaction (AI) during which repeated contact is made by one or both males. This is usually preceded by a threat period during which males exchange non-contact threats (for further details see: Twiss 1991).
Roll	Usually seen after a fight or chase, male turns on his dorsal-ventral axis. Suggested as a form of locomotion or a 'victory roll' (Twiss 1991, Lawson 1993).
Body Slap	A male pushing his body off the ground and slamming his ventral surface back down onto the substrate. Usually performed in multiple repetitions per bout (Bishop et al. 2014).
Reproductive behaviours	
Approach Female	A subgroup of general locomotion, approach refers to direct movement of a male towards a female.
Non-Aggressive Flippering	Male slowly strokes the flank of the intended mate with his or her flipper. Usually seen prior to mounting or during male positioning. (*Abbrev:* Non-Ag Flip)
Attempted copulation	Attempted copulations begin when a male attempts to get his fore-flippers on the female's back and grabs the scruff of her neck with his jaws (Twiss 1991). This behaviour has also been called a "mount" (Boness 1984).

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Copulation	Following the attempted copulation/mounting behaviour, the male will attempt intromission—if successful this is the point in which actual copulation commences. If the copulatory embrace post-intromission persists for a minimum of 10min the copulation is classified as 'successful'. From previous studies (Twiss 1991) 'successful' copulations last on average 15-20m and we assume that if shorter than 10 min, it is unlikely that insemination will occur.
Unsuccessful copulation	Copulations which do not last for longer than 10 minutes post intromission are considered unsuccessful. 'Unsuccessful copulations' indicate the male achieved intromission but lost contact with the female after a short period of time and the cause of the interruption was recorded.
Other	
Rest	Non-active state. Head down, eyes may be open or closed.
Comfort Move	General repositioning, scratching or flipper-movements which stationary. Eyes may be open or closed and head may be off the ground.
Alert	Cases where a male is clearly observant, head raised, or gaze directed.
Locomotion	Movement around the colony without directed approach towards a female or male. Change in geographic location.
Out of Sight	Where a male is not visible from the hide (due to topography or range of view) but is known to still be present in the study site.

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